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HABITAT PREFERENCES OF THE TAWNY OWL (*STRIX ALUCO*) IN A SPECIAL CONSERVANCY AREA OF EASTERN SPAIN

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Abstract.—The Tawny Owl (*Strix aluco*) is the most abundant nocturnal raptor in Europe. It has been thoroughly studied in various regions, but its habitat preferences in Mediterranean environments remain poorly understood. With the aim to present novel information about this aspect of the ecology of the Tawny Owl, we established 115 survey stations in the Special Conservancy Area "Sierras de Talayuelas y Aliaguilla" (Castilla–La Mancha region, eastern Spain) and carried out nocturnal surveys by recording spontaneous calls and vocal responses to call playbacks. We then assessed environmental characteristics (vegetation types, soil type, altitude, potential competitors, and anthropic disturbance) in areas where owls were detected or not detected during the breeding season. Overall, we detected 60 responding owls at 49 survey stations during breeding season in the study area (i.e., density 1.22 owls/km^2). We found that Tawny Owls preferred lower altitudes and patchy heterogeneous areas. Owls seemed to avoid natural grasslands and areas characterized by limestone soils and associated vegetation, and preferred areas characterized by clay soils and associated vegetation. Interestingly, we did not detect owls close to wind farms, which seem to create a buffer effect on owls' occurrence. The noise generated by the turbines might be a limiting factor that could account for this avoidance. Our multivariate results showed that Tawny Owls preferred heterogeneous patchy habitat but avoided non-irrigated arable land. Tawny Owls inhabit Mediterranean landscapes where conditions are favorable, but human activities such as wind farms may limit their distribution. Additional research is needed to determine the drivers of this avoidance and whether Tawny Owls also avoid wind farms in other regions of their range.

Key Words: *Tawny Owl*; Strix aluco; *conservation*; *habitat selection*; *Mediterranean*; *nocturnal raptors*; *owls*; *renewable energy*; *wind farms*.

PREFERENCIAS DE HÁBITAT DE *STRIX ALUCO* EN UNA ZONA DE ESPECIAL DE CONSERVACIÓN DEL ESTE DE ESPAÑA

Resumen.—*Strix aluco* es la rapaz nocturna más abundante en Europa. La especie ha sido extensamente estudiada en varias regiones, pero sus preferencias de hábitat en ambientes mediterráneos siguen poco estudiadas. Con el objetivo de presentar nueva información sobre este aspecto de la ecología de *S. aluco*, establecimos 115 estaciones de muestreo en la Zona Especial de Conservación "Sierras de Talayuelas y Aliaguilla" (región de Castilla–La Mancha, este de España) y realizamos muestreos nocturnos mediante el registro de llamadas espontáneas y respuestas vocales a reclamos. A continuación, evaluamos características ambientales (tipos de vegetación, naturaleza del suelo, altitud, competidores potenciales, molestias antrópicas) en áreas donde los búhos fueron detectados o no detectados durante la estación reproductora. En total, detectamos 60 *S. aluco* que respondieron en 49 estaciones de muestreo durante el período

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reproductor en el área de estudio (i.e., densidad de 1.22 búhos/km^2). Encontramos que *S. aluco* prefirió altitudes más bajas y áreas heterogéneas en parche. Los *S. aluco* parecieron evitar los pastizales naturales y las áreas caracterizadas por suelos calizos y su vegetación asociada, mientras que prefirieron áreas caracterizadas por suelos arcillosos y su vegetación asociada. Curiosamente, no detectamos *S. aluco* cerca de parques eólicos, los cuales parecieron crear un efecto tampón en la presencia de *S. aluco*. El ruido generado por las turbinas sería un factor limitante que podría explicar esta ausencia. Nuestros resultados mostraron que *S. aluco* prefirió hábitats heterogéneos y parcheados, pero evitó los suelos de agricultura de secano. *S. aluco* habita paisajes mediterráneos donde las condiciones son favorables, pero las actividades humanas como los parques eólicos pueden limitar su distribución. Se necesita investigación adicional para determinar las razones de esta ausencia en los parques eólicos y si *S. aluco* también los evita en otras regiones de su área de distribución.

[Traducción de los autores editada]

INTRODUCTION

Reproduction is a critical process in which breeders generally invest a lot of energy through parental care, resulting in a trade-off between survival and reproduction (Trivers 1972, Santos and Nakagawa 2012). Organisms must select breeding territories where their biological requirements can be fulfilled. Thus, the selection of an adequate breeding territory is crucial for successful reproduction (Korpimäki 1988). However, reproduction of birds in general and raptors in particular may be threatened by different factors including predation of the adults or young (Atuo and O'Connell 2018), intraspecific and interspecific competition (Lourenço et al 2013), limited resource availability (Furness and Birkhead 1984), and direct or indirect human disturbance (Garcês et al. 2019). In order to avoid or reduce these hazards, territorial species selecting their breeding areas attend to different environmental features, including natural characteristics and human alterations. This is also the case for nocturnal raptors (Order Strigiformes), territorial birds that select and defend a breeding area in order to maximize their breeding success.

In Europe, particularly in Spain, the Tawny Owl (*Strix aluco*) is one of the most studied nocturnal raptors in relation to habitat selection and territory defense (Redpath 1994, 1995, Appleby and Redpath 1997, Zuberogoitia and Martínez 2000, Vrezec and Tome 2004a, 2004b, Sunde and Redpath 2006, Zuberogoitia et al. 2019, and references therein). This species shows huge niche plasticity (Vrezec and Tome 2004a). However, despite having a broad versatility in habitat selection (Marchesi et al. 2006), the Tawny Owl's presence correlates with the area of natural forests and wooded areas (Sánchez-Zapata and Calvo 1999, Bartolommei et al. 2013, Fröhlich and Ciach 2018). Tawny Owls prefer wooded areas and their edges, finding their optimal habitat in medium-sized and fragmented forests (Redpath 1995). Although there is a vast literature about this species' territory selection in Europe, most studies have been focused in non-Mediterranean areas with different environmental conditions, including vegetation (e.g., deciduous forests) and climatic conditions (i.e., Atlantic; Galeotti 1990, Redpath 1994, 1995, Appleby and Redpath 1997, Zuberogoitia and Martínez 2000, Vrezec and Tome 2004a, 2004b, Sunde and Redpath 2006, Romanowski and Żmihorski 2009, Rumbutis et al. 2017). For this reason, we here present data to fill a gap in the knowledge of the breeding ecology of this species. In this study, our aim was to explore the environmental and anthropic variables determining habitat preferences of the Tawny Owl in a Special Conservancy Area in the eastern Iberian Peninsula. We assessed the relationship between owl occurrence and habitat features in Mediterranean forests, and we discussed anthropogenic factors limiting Tawny Owl distribution in the study area.

METHODS

Study Area. We studied Tawny Owls in the Special Conservancy Area "Sierras de Talayuelas y Aliaguilla" (hereafter ZEC), which is part of the Natura 2000 network (code ES4230002). This area is located in Castilla–La Mancha region, eastern Spain (coordinates: 39°46.733′N, 1°16.150′W; area = 115 km^2; Fig. 1). The vegetation is primarily forest, with tree species varying depending on soil composition, which is siliceous or calcareous. On siliceous areas below 1400 masl, vast areas of maritime pine (*Pinus pinaster*) are interspersed with some gall oaks (*Quercus faginea*). Above 1400 masl, scattered Scots pines (*Pinus sylvestris*) and Pyrenean oaks (*Quercus pyrenaica*) dominate. The undergrowth consists primarily of different rockrose species (*Cistus ladanifer, C. laurifolius, C. populifolius, C. salvifolius, C. clusii*) and heather species (*Erica arborea, E. cinerea, E.*

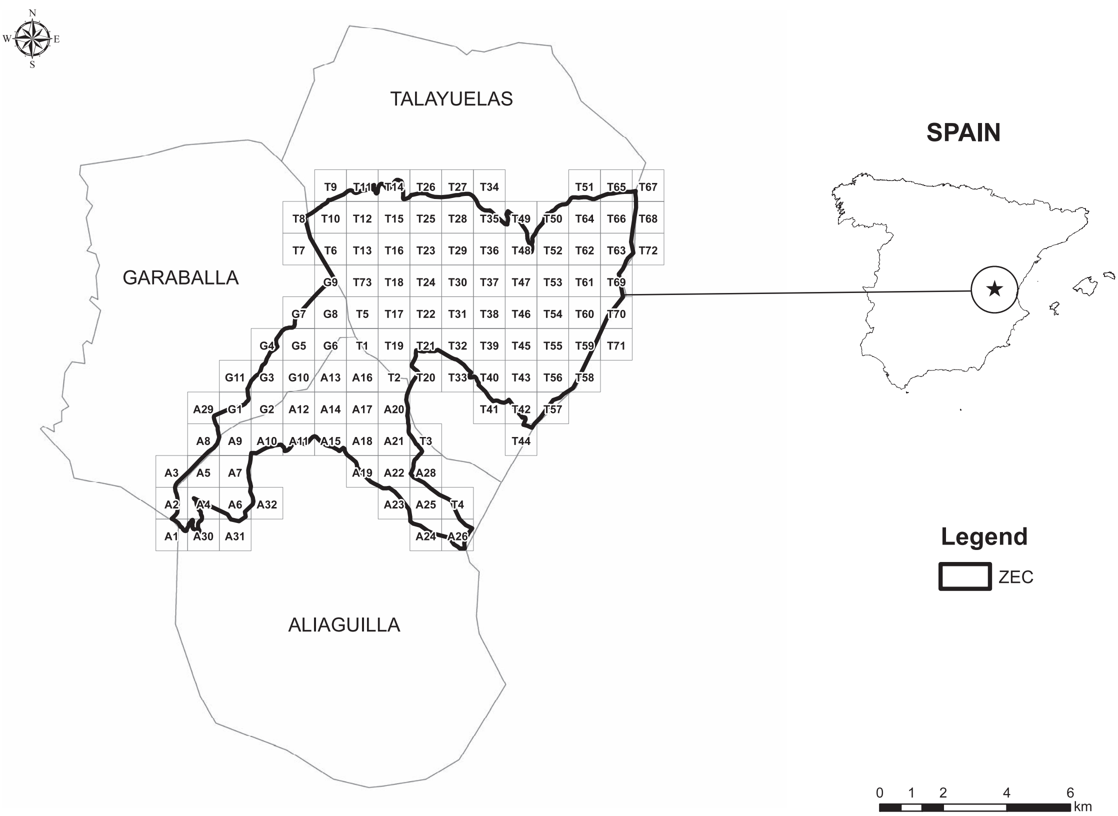

Figure 1. Location of the study area in Spain (right) and grid of 1 km × 1 km squares used for surveys of Tawny Owls (left).

multiflora, and *Calluna vulgaris*). In contrast, in calcareous areas at lower altitudes, forests contain mainly Aleppo pines (*Pinus halepensis*) and holm oaks (*Quercus ilex*), whereas the Austrian pine (*Pinus nigra*) occurs at higher altitudes. The undergrowth is mainly dominated by dense shrubby kermes oaks (*Quercus coccifera*), accompanied by other species including sunrose (*Cistus albidus*), rosemary (*Rosmarinus officinalis*), laurustinus (*Viburnum tinus*), and gorses (*Ulex parviflorus* and *Genista scorpius*). Soil lithology has an important effect on water availability (Acosta et al. 2008), which is much higher in siliceous soils and very low in calcareous areas, and that, in turn, affects prey availability for owls (Torre and Arrizabalaga 2008, Rosalino et al. 2011).

In general, this area has relatively young forests, traditionally and currently dedicated to timber and resin harvest. Moreover, in this area local residents obtain other benefits from the forests, which serve as places to collect edible mushrooms and carry out apiculture, hunting, leisure activities such as hiking and climbing, and traditional low-density livestock-rearing. Between wooded areas there are small open areas where non-irrigated cereals and vineyards are cultivated.

The climate is Mediterranean with continental traits, but with some maritime influence (large water accumulation due to mist). Winters are cold, with frequent frosts and eventual snows. Spring and autumn are moderately humid, but summer is dry and hot. Average annual precipitation is 587.1 mm and average annual temperature is 12.3°C (Dirección General de Montes y Espacios Naturales 2015).

Study Species. The Tawny Owl is the most abundant nocturnal raptor in Europe (König and Weick 2008). A medium-sized owl with mass around 400–600 g (König and Weick 2008), it is well-known for its strong territorial behavior and territory fidelity (Southern 1970, Hirons 1985, Sunde and Bølstad 2004). This species perches in trees while hunting

(Mikkola 1983) and nests in cavities, other species' nests (Redpath 1995, Sunde and Redpath 2006), or occasionally on human-made structures such as buildings (Zuberogoitia 2011). The Tawny Owl consumes mostly small mammals, but also birds, amphibians, and reptiles (Cramp 1985). In our study area, Tawny Owls begin courtship and pre-breeding activities from October to January, incubation takes place between February and April, nestlings hatch between May and July, and the post-fledging period occurs from July to October.

Surveys. We divided the study area into 1 km × 1 km squares (sampling units) using the national 1-km^2 Universal Transverse Mercator (UTM) grid division, obtained from the Spanish National Center of Geographic Information (https://www.cnig.es/home). We included every square containing part of the ZEC (115 squares in total). In each 1 km^2 square, we established one survey station. To select each survey station's location, we followed Worthington-Hill and Conway's (2017) methodology: survey stations were located on roadways or tracks accessible by a 4-wheel-drive vehicle and as close to the center of the square as possible. Due to the dearth of suitable roadways in some squares, we excluded nine squares (7.8% of total area) and not every station could be placed close to the center of the square. According to Zuberogoitia and Campos (1998), survey stations should be placed 500–1000 m apart in wooded and sloped mountain areas, given suitable terrain and access. At ZEC, survey stations were >200 m and <1800 m apart, covering all the accessible areas of the study area. We conducted surveys when wind speed was <20 km/hr and precipitation did not occur (Lengagne and Slater 2002, Zuberogoitia et al. 2019). We began surveys 30 min after sunset and finished by midnight.

Our survey protocol included both listening for spontaneous calls and broadcasting conspecific calls (Bibby et al. 2000, Haug and Didiuk 1993, Zuberogoitia and Campos 1998), as well as broadcasting calls of a predator species. Specifically, our survey protocol was as follows: (1) wait 5 min after arrival at the survey station (to avoid disturbance induced by researchers' vehicle), (2) listen for spontaneous Tawny Owl calls for 5 min, (3) broadcast Tawny Owl calls for 3 min, (4) listen for response calls of Tawny Owls for 5 min, (5) broadcast calls of the Eurasian Eagle-Owl (*Bubo bubo*), a competitor and potential predator of our target species (Lourenço et al. 2013, Penteriani and Delgado 2019) for 3 min, (6) listen for calls of both owl species for 5 min. Total time per survey was 26 min. Every survey was performed by two researchers. Calls were broadcast from a 2018 Dacia Duster's speakers, with the vehicle's doors open. Calls were obtained from Xeno-Canto project (www.xeno-canto.org); we used the male Tawny Owl call "XC412453" and the Eurasian Eagle-Owl call "XC304909." For each survey station, we recorded the species (i.e., Tawny Owl and/or Eurasian Eagle-Owl), sex, and total number of owls that responded (at any point during the survey). We only recorded male calls and we assumed that every responding owl represented a breeding bird during our winter-spring survey. If two or three owls responded at a single survey station from different places during a short time interval, we considered that at least two or three breeding pairs could be in the sampling unit.

Although Tawny Owls are residents and territories are maintained year-round (Southern 1970, Percival 2002), the vocal activity of the Tawny Owl varies throughout the year. According to Zuberogoitia and Martínez (2000), the best time to detect breeding territorial birds using playback calls spans from December to March in our area, but owls' spontaneous calling peaks from March to April (Zuberogoitia et al. 2019). Thus, we surveyed the entire ZEC study area twice: once in October-December (hereafter autumn) and once in February-April (hereafter winter-spring).

Habitat Characterization. Field data were mapped using ArcGIS 10.7 (Esri 2019) software with different information layers obtained from the Spanish National Institute of Geography (https://www.ign.es). We used Corine Land Cover (CLC) 2018 (https://land.copernicus.eu/) to characterize the vegetation of each square by the types of vegetation present, and the area and number of patches of each vegetation type in the area. CLC discriminates among broad vegetation categories (e.g., coniferous forest vs. mixed forest) but not among species forming these patches. Therefore, we added a lithology layer to improve our analyses, because there is a strong relationship between vegetation types and lithology (Vilà et al. 2007). We downloaded data from the National Geology Map project (Mapa Geológico Nacional, MAGNA 50; pages 637 and 665), available at the Spanish Institute of Geology and Mining (http://www.igme.es/). We simplified the information on these maps to seven broad categories of soils derived from different bedrocks: schists and shales, quartzites, conglomerates, sandstones, limestones, loams, and clays. In addition, we considered altitude of the survey

Table 1. Variables used to characterize habitat preferences of Tawny Owls in a Special Conservancy Area of eastern Spain.

CATEGORY	VARIABLE	ABBREVIATION[a]	TYPE	UNITS
Landscape	Non-irrigated arable land	clc211	Continuous	km^2
	Vineyards	clc221	Continuous	km^2
	Complex cultivation patterns	clc242	Continuous	km^2
	Land principally occupied by agriculture, with significant areas of natural vegetation	clc243	Continuous	km^2
	Coniferous forest	clc312	Continuous	km^2
	Mixed forest	clc313	Continuous	km^2
	Natural grasslands	clc321	Continuous	km^2
	Sclerophylls vegetation	clc323	Continuous	km^2
	Transitional woodland-shrub	clc324	Continuous	km^2
	Number of vegetation patches per square	Patches	Continuous	0,1,2...
	Number of different CLC codes per square	Habitats	Continuous	0,1,2...
Geomorphology	Schists and shales	rc1	Continuous	km^2
	Quartzites	rc2	Continuous	km^2
	Conglomerates	rc3	Continuous	km^2
	Sandstones	rc4	Continuous	km^2
	Limestones	rc5	Continuous	km^2
	Loams	rc6	Continuous	km^2
	Clays	rc7	Continuous	km^2
	Altitude	Altitude	Continuous	masl
Disturbance	Presence/absence of paved road in the square	Road	Categorical	0/1
	Presence/absence of paved road in contiguous squares	Road_cont	Categorical	0/1
	Presence/absence of wind farms in the square	Wind-farm	Categorical	0/1
	Presence/absence of wind farms in contiguous squares	Wind-farm_cont	Categorical	0/1
	Presence/absence of wind farms in 2-km contiguous squares	Wind-farm_2_cont	Categorical	0/1
Competition	Presence/absence of Eurasian Eagle-Owls in the square	EEO	Categorical	0/1
	Presence/absence of Eurasian Eagle-Owls in contiguous squares	EOO_cont	Categorical	0/1

[a] CLC = Corine Land Cover.

station, the presence of human disturbance factors (i.e., roads and wind farms), the presence/absence of potential competitors (i.e., Eurasian Eagle-Owl) in the square or in surrounding (contiguous) squares in our field survey, and habitat fragmentation measured by number of different habitat codes per square and number of different vegetation patches (Table 1).

Statistical Analysis. To analyze which variables could determine habitat preferences, we first performed nonparametric univariate tests (i.e., Mann-Whitney and Kruskal-Wallis) to assess differences in both detection (presence/absence) and owl density. Tawny Owl density was classified as one of three categories: "Null" (0), "Low" (one responding individual per square), or "High" (two or three individuals per square), the latter including two and three individuals to avoid the statistical bias of unbalanced groups because of the few squares with three Tawny Owls detected. We tested only the survey data we recorded during the winter-spring survey, because we assume this better represents the areas used by breeding birds.

We then fitted logistic mixed effects models (a particular case of Generalized Linear Mixed Models, GLMMs) to analyze habitat preferences using the lme4 R package (Bates et al. 2015). We grouped the variables by categories (i.e., landscape, geomorphology, disturbance, and competition; Table 1) and tested them against Tawny Owl presence/absence. The 1 km $\times$ 1 km square code was included as random factor in all models. We included those variables that showed significant differences in Tawny Owl presence or absence in univariate tests

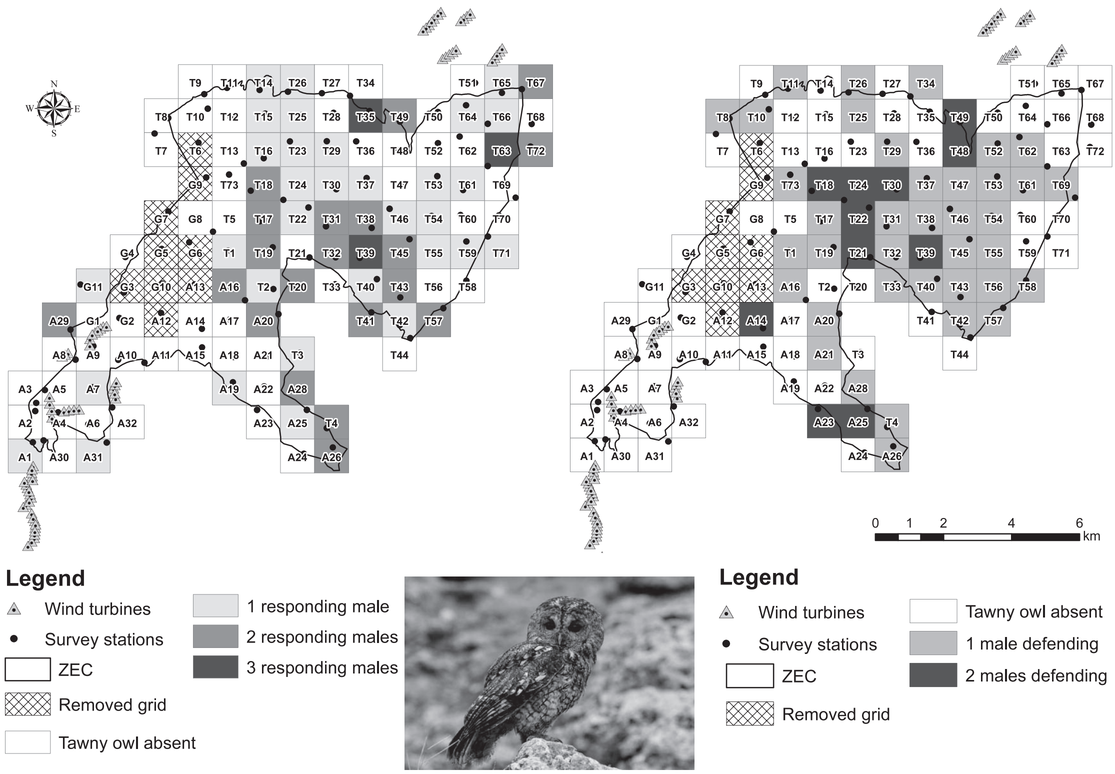

Figure 2. Distribution and abundance of the Tawny Owl in the Special Conservancy Area "Sierras de Talayuelas y Aliaguilla" (Castilla – La Mancha, eastern Spain) in autumn (left) and winter-spring (right).

and built GLMMs with them. We modelled each set of variables grouped by category separately and then the combination of all categories. We ranked models according to the Akaike Information Criterion (AIC) score (Akaike 1974). Models with ΔAIC < 2 were considered the best models. We also computed the AIC weight (AIC$_w$) of each mode (Burnham and Anderson 2002). All statistical analyses were done with R version 3.6 (R Core Team 2019) and Statistica version 8.0 (StatSoft, Inc. 2007).

Results

Spatial Distribution and Abundance. Overall, we surveyed 106 squares (92.2% of the total area of the study area; Fig. 2). Our survey effort included 92 hr of surveys. By period, we detected at least one Tawny Owl in 55 squares (51.9 %) during the autumn surveys, and in 49 squares (46.3%) during the winter-spring surveys, a difference of 11% ($\chi^2 = 5.611$, df $= 1$, $P = 0.018$). Although most of our study area was covered by forests, we did not detect Tawny Owls in many areas, and there were differences in the pattern of occupation between the autumn and winter-spring surveys (Fig. 2).

We detected 81 male Tawny Owls in 55 squares in the autumn (1.47 owls per sampling unit where owls were detected). Because sampling units were 1 km^2, we estimated owl density as 1.47 owls/km^2, considering only the squares where owls were detected. In the winter-spring survey, we detected fewer owls: 60 males in 49 squares (1.22 owls per sampling unit where owls were detected, or 1.22 owls/km^2). When we included the entire study area surveyed (106 squares), estimated densities were 0.76 owls/km^2 in autumn and 0.57 owls/km^2 in winter-spring We estimated the number of breeding pairs detected within the entire study area as 60, based on male calls.

Using only the winter-spring information, which we assumed represents breeding habitat selection, our univariate tests with presence/absence data showed that Tawny Owls seemed to prefer lower altitudes and more fragmented areas (Table 2). Owls avoided natural grassland and areas with limestone

Table 2. Univariate comparison of 1 km × 1 km squares where Tawny Owls were detected or not detected in the study area during the winter-spring survey. Significant variables are highlighted in bold. Variables defined in Table 1.

VARIABLE TYPE	VARIABLE ABBREVIATION	STATISTIC	P-VALUE
Landscape	clc211	1271.5	0.365
	clc221	1305.0	0.233
	clc242	1342.0	0.548
	clc243	1359.5	0.674
	clc312	1328.0	0.666
	clc313	1349.0	0.736
	clc321	1711.5	**0.022**
	clc323	1344.5	0.708
	clc324	1177.0	0.153
	Patches	980.0	**0.007**
	Habitats	1106.0	0.062
Geomorphology	rc1	1276.0	0.255
	rc2	1367.5	0.805
	rc3	1169.0	0.091
	rc4	1593.0	0.207
	rc5	1952.0	**<0.001**
	rc6	1507.0	0.460
	rc7	702.0	**<0.001**
	Altitude	2073.5	**<0.001**
Disturbance	Road	4.789	**0.029**
	Road_cont	11.628	**<0.001**
	Wind-farm	6.382	**0.012**
	Wind-farm_cont	20.991	**<0.001**
	Wind-farm_2_cont	29.336	**<0.001**
Competition	EEO	0.405	0.524
	EOO_cont	1.040	0.308

soils, but preferred areas with clay soils (Table 2). Relative to human disturbance, Tawny Owls avoided areas of wind farms. There were significant differences between squares with and without owl detections in all three related wind-farm variables: wind-farm presence/absence in the square, in the contiguous squares, and in the 2-km contiguous squares (Table 2). We found a positive relationship between roads and Tawny Owl occurrence in two related variables: road presence/absence within the square and within the contiguous squares (Table 2). In relation to potential competitors, we detected eagle-owls at seven and two sampling units in autumn and winter-spring, respectively. Interestingly, in all sampling units where eagle-owls were detected, Tawny Owls were detected as well.

In winter-spring surveys, Tawny Owls were detected at higher numbers at lower altitude (nonparametric univariate tests; $H_{2,106} = 18.424$, $P = 0.001$) with clay ($H_{2,106} = 23.342$, $P < 0.001$) and limestone soils ($H_{2,106} = 13.957$, $P = 0.001$), and in heterogeneous ($H_{2,106} = 7.720$, $P = 0.021$) and fragmented environments ($H_{2,106} = 8.528$, $P = 0.014$).

The best model to account for habitat preferences was the one that included geomorphology, landscape, and disturbance variables (Table 3). This model explained 74.5% of the total variance. However, the only significant predictors were two landscape features: Tawny Owls preferred areas with many vegetation patches and avoided non-irrigated arable lands (Table 4).

DISCUSSION

Our study showed the importance of environmental factors and human disturbance for habitat selection of the Tawny Owl in Mediterranean landscapes. We found that vegetation, soil nature, altitude, environmental heterogeneity, and disturbance caused by human infrastructure helped explain the distribution and abundance of the Tawny Owl in our study area. The role of wind farms may be important, reducing the available area for

Table 3. Model selection results of the logistic mixed effects models of Tawny Owl's habitat preferences during the winter-spring survey ranked according to AIC values. Abbreviations: df = degrees of freedom, LogLik = log likelihood, AIC = Akaike information criterion; AIC_w = Akaike weight.

MODEL	DF	LOGLIK	AIC	ΔAIC	AIC_w
Geomorphology + Landscape + Disturbance	16	−37.239	106.478	0.000	0.859
Landscape + Disturbance	11	−44.269	110.538	4.061	0.113
Geomorphology + Landscape	11	−45.731	113.462	6.985	0.026
Disturbance	7	−52.216	118.433	11.955	0.002
Geomorphology + Disturbance	12	−49.258	122.516	16.038	0.000
Landscape	6	−61.496	134.993	28.515	0.000
Geomorphology	7	−60.910	135.821	29.343	0.000
Null model	2	−73.171	150.343	43.865	0.000

Table 4. Results of the best logistic mixed effects model of habitat preferences of the Tawny Owl in eastern Spain during the winter-spring survey. The model included geomorphology, landscape features, and disturbance as dependent factors. Significant predictors are highlighted in bold.

VARIABLE	ESTIMATE	STD. ERROR	*Z*	*P*-VALUE
(Intercept)	2.087	4.181	0.499	0.618
Conglomerates	−4.216	2.504	−1.684	0.092
Sandstones	−0.100	1.276	−0.078	0.938
Limestone	−1.969	1.705	−1.155	0.248
Clays	1.233	1.529	0.806	0.420
Altitude	−0.004	0.004	−1.008	0.313
Habitats	−0.119	0.316	−0.376	0.707
Patches	1.086	0.545	1.993	**0.046**
Non-irrigated arable land	−8.447	2.714	−3.112	**0.002**
Natural grasslands	−6.854	3.899	−1.758	0.079
Road	−0.761	1.017	−0.748	0.454
Contiguous road	1.058	0.865	1.223	0.221
Wind farm	−6.096	2518689.829	0.000	1.000
Contiguous wind farm	2.363	340830.828	0.000	1.000
2-km contiguous wind farm	−27.509	330238.704	0.000	1.000

this species as a consequence of a potential buffer effect (Pearce-Higgins et al. 2009).

Spatial Distribution and Abundance. In contrast to previous studies that showed the Tawny Owl is most vocal during incubation (Zuberogoitia et al. 2019), we found a slight decrease in the number of owls detected during the winter-spring surveys in comparison to the autumn surveys. Two potential explanations could account for these results. In autumn, adult males (that may eventually breed) and young males (floaters) may call or respond to call broadcasts, but by winter-spring, the floaters may no longer respond (Appleby and Redpath 1997). In addition, Tawny Owls' nonbreeding-season territories are 50% larger than breeding-season territories (Sunde et al. 2001), so individual birds in our study may respond from more blocks in the autumn and fewer by winter-spring when territories contract. Furthermore, considering the territorial nature of the Tawny Owl (Redpath 1994), intraspecific competition between males to defend the territories could lead to the expelling of subordinate males, thus decreasing the average density found in the winter-spring survey in comparison to the autumn survey.

The breeding season population density we estimated (0.57 pairs per km^2 in the entire study area and 1.22 pairs per km^2 within the squares where owls were detected) was relatively low in comparison to the mean densities (between 0.2 and 5 pairs per km^2) reported by other authors in Europe (Southern 1970, Galeotti 1994, Galeotti and Pavan 1993, Hirons 1985, Redpath 1994, Jedrzejewski et al. 1996, Sánchez-Zapata and Calvo 1999). Several factors may influence this. First, we surveyed each sampling unit only one time in autumn and one time in winter-spring, and did not search for nests or determine detectability, so it is likely that we did not detect all owls in our study area. In addition, this species' reproductive rate varies with the abundance of cyclic microtid rodents, such that its reproductive rate is low in one of every three years (Francis and Saurola 2004); if our one-year study was conducted in a year of low rodent abundance, then detection of owls calling or responding to playbacks might also have been low.

Habitat Preferences. Our results both of the univariate comparisons and the GLMMs showed that Tawny Owls preferred areas at lower altitude, with greater habitat fragmentation, non-irrigated arable lands, and areas without natural pastures (as observed by Brambilla et al. 2020) on clay soils. According to Vrezec and Tome (2004b), the Tawny Owl in central Slovenia has no altitude limitations for breeding territories, and when it avoids higher-elevation study areas it is due to competitive exclusion by other larger nocturnal raptors such as the Eurasian Eagle-Owl. In our study area, we did not find an effect of Ural Owl (*Strix uralensis*) occurrence on Tawny Owl distribution; however, we detected few eagle-owls overall. Other factors might keep the Tawny Owl from inhabiting higher altitudes, such as the lower height of the vegetation, the presence of wind turbines (all of which are placed along the top of mountain ridges), or lower temperatures, which may affect prey availability. For example, in the Duna-Ipoly National Park (Hungary), Tawny Owls select higher elevations, but this study was done at lower elevations (Sasvári and Hegyi 2011). In our case, our results showed a selection of intermediate conditions, either because of the vegetation of those areas and/or less human disturbance.

In our study area, Tawny Owls were detected in areas with higher heterogeneity of vegetation types (i.e., based on the different codes of the CLC) and more ecotones. This result is consistent with Fröhlich and Ciach (2019) who found that environmental heterogeneity and habitat fragmentation are characteristics that maximize the richness of niches for different micromammals and increase food availability, thus increasing the diversity of owls and their abundance. Moreover, Tawny Owl detection was low in areas with natural pastures. This was an expected result considering that this species needs trees for hunting and breeding, and that open areas could represent low-quality hunting habitats (Redpath 1995, Sunde and Redpath 2006). In addition, other studies showed that Tawny Owl diet is more diverse in forest areas (Romanowski and Żmihorski 2009). Therefore, it seems that large grassland areas could prevent Tawny Owls from establishing territories.

Because of the correlation between vegetation and lithology, we concluded that owls avoided Aleppo pine forests (on limestone soils) and preferred maritime pine forests (on siliceous soils). Avoidance may be driven by different factors, such as differences in vegetation associated with water availability in each soil type and its impact on the corresponding micromammal community (e.g., a reduced availability of adequate substrates for burrows or shelters). If the vegetation of limestone areas is less favorable for prey, this could have an indirect effect on the Tawny Owl. This could also have other effects in terms of fewer suitable nesting spots, or the occurrence of other species that may compete for resources (e.g., forest raptors that prefer limestone areas; e.g., Brambilla et al. 2020). In our study area, dense shrubby kermes oaks on limestone soils cover large areas and likely reduce hunting areas for the Tawny Owl.

We found evidence that the presence of wind turbines negatively affects Tawny Owl presence during the breeding season in a radius of up to 2 km, at least in our univariate comparisons. Wind-farm management considers the lethal effect of turbines, but does not consider indirect effects, including negative buffer effects (Pearce-Higgins et al. 2009), noise disturbance (Madders and Whitfield 2006), and changes in the landscape (Beston et al. 2016). Noise can disturb animal communication by reducing the receiver's ability to capture important information as background noise increases, a process termed "acoustic masking" (Francis et al. 2011). This acoustic masking could reduce the success of owls attempting to find a mate and establish a territory (Bayne et al. 2008, Francis et al. 2009, Francis and Barber 2013, Shannon et al. 2016, Shonfield and Bayne 2017). In addition, the effect of noise on nocturnal predators decreases hunting success by reducing their chance of detecting prey (Mason et al. 2016, Ciach and Fröhlich 2017, Fröhlich and Ciach 2018). This buffer effect could explain the avoidance of the area around wind farms and may agree with other studies in which anthropogenic noise affects animal behavior, distribution, and reproductive success (Francis and Barber 2013).

In addition, the installation of wind turbines also entails changes in the landscape such as increased erosion and drying of the areas in which wind turbines are located (Beston et al. 2016), causing a loss of plant cover. This effect could be transferred to the Tawny Owl via the food web, by decreasing prey availability. The Tawny Owl feeds mainly on micromammals (Cramp 1985), which are closely linked to the plant cover in the undergrowth. Hence, a decrease in the herbaceous canopy could lead to a significant reduction in the abundance and diversity of these prey.

We also found a significant relationship between the presence of roads in a square or the neighboring ones and the occurrence of Tawny Owl, at least in our univariate comparisons. However, it is curious that this relationship was positive. This positive relationship was counterintuitive given the negative effects of roads relative to noise disturbance (Gomes et al. 2009, Hindmarch et al. 2012, Silva et al. 2012, McClure et al. 2013, Senzaki et al. 2016), pollutants, and collisions with vehicles (Fahrig and Rytwinski 2009). Traffic noise can reduce hunting efficiency of nocturnal raptors (Senzaki et al. 2016). Roads modify behavior and reduce the connectivity of populations in some nocturnal birds (Grilo et al. 2014) and road habitats may represent poorer quality areas for owls (Silva et al. 2012). Our results might be explained by the small sample size (17 squares with presence of road and 21 with roads in the neighboring square), together with the presence of favorable areas (low altitude, high heterogeneity, and clay soils) in the vicinity of the road, and very low vehicle traffic at night. In addition, there may be a link between roads and associated areas for rest and recreation where drivers stop to eat; in these areas, the accumulation of organic waste could enhance the populations of micromammals and, consequently, their predators too.

Conclusions. Our results show that Tawny Owls prefer lower-altitude areas of higher habitat heterogeneity during the breeding season. Owls were not detected in large areas surrounding wind turbines, potentially because of noise disturbance or reduced prey populations, but this needs more study. Given the important role of habitat characteristics on owl presence, we recommend that managers and developers consider the avoidance effect caused by wind farms in future planning of power infrastructure in Mediterranean ecosystems in order to avoid negative effects on owls.

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